

Bacterial Endophytes, a resilient way toward sustainable agriculture: provide plant growth promotion and biocontrol of plant pathogens

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Plant pathogens are considered a major constraint in decreasing the quality and quantity of plants and plant products by attacking the seed from its germination to the harvesting stage. To date, various multifunctional chemical pesticides have been applied to control these infectious entities, but these chemical pesticides are not as effective in controlling them. That is why "bacterial endophytes," an alternative to these chemical pesticides, have been determined in the history of mankind through multidisciplinary ways. At the same time, these endophytes work to save the living environment, improve plant growth, and control infectious plant pathogens. The current study summarizes and analyzes the pioneering and recent works on plant bacterial endophytes and their mechanisms as biocontrol agents/plant growth promotion, interaction with the host plant, root colonization, systemic colonization of aerial plant tissues, phytohormone production and modulation, host specificity, genes expressed in the endosphere, multi-omics approaches to improve endophyte use, and biopesticide formulation by these bacterial endophytes. The manuscript highlights the most necessary information about bacterial endophytes, and the study will play a vital role in the further use and handling of these bacterial endophytes for sustainable agricultural production.

Keywords: Bacterial endophytes, Plant-associated bacteria, Systemic colonization, Induction of systemic response, δ -endotoxins, Multi-Omics approaches.

INTRODUCTION

Fruits and vegetables, being important food crops, are affected by various plant diseases, resulting in massive yield losses during cultivation, handling and transportation until storage (El Khetabi *et al.*, 2022; Ali *et al.*, 2022b; Anwar *et al.*, 2022). Different control measures are used to manage these destructive agricultural diseases, including the application of synthetic fungicides, which have an excellent ability to control plant diseases. But, due to their high environmental pollution and high costs, these are not considered for further applications (Tabbasum *et al.*, 2022). So, for sustainable agriculture production and less use of these harmful synthetic fungicides, we need to come up with ways to control diseases that are cheap, safe for the environment, and very effective. The most exported things on the market right now are organic vegetables and fruits. To improve their production, they need to use new technologies instead of

chemicals. In this case, the most effective alternative to synthetic fungicides is the use of microbial biocontrol agents (Onwe *et al.*, 2022; Hammami *et al.*, 2022). These beneficial microorganisms, both fungi and bacteria, are found inside the plant and are termed endophytes. Many microorganisms readily develop symbiotic relationships with plants, providing them with different benefits, including bacteria (Cui *et al.*, 2022). Approximately 300,000 species of plants develop symbiotic associations with one or more endophytic species. These endophytic bacteria provide different benefits to plants, such as plant growth promotion, tolerance against stress conditions, resistance against biotic and abiotic factors, availability of plant nutrients, and production of allelopathic effects on other competing plant species. Thus, these endophytes improve the survival of plants against biotic and abiotic factors. Endophytic bacteria have been found in a wide range of plant hosts, including prairie plants, agronomic

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plants, perennials, and wild plants (Renugadevi *et al.*, 2021; Riva *et al.*, 2022).

For the management of plant diseases, different endophytic bacteria are employed that reduce the harmful effects of pathogens (Ustiatik *et al.*, 2022; Devi *et al.*, 2022). These endophytic bacteria are also the plant growth-promoting bacteria (PGPB) that develop beneficial associations with various plant species and promote plant growth by stimulating the acquisition of nutrients by plants, like the mobilization of immobile forms of iron by the production of siderophores and phosphorus by organic acids, and also improving biological nitrogen fixation (Wang *et al.*, 2022; Abid *et al.*, 2022). These bacteria can improve the plant's growth directly and indirectly and can develop associations both internally and externally within the host plant. In the case of external associations, bacterial species live outside the host, in the rhizosphere, where they colonize the plant roots in soil or on the leaf surface and are called epiphytic bacteria. In contrast, endophytic bacteria are those that live inside the host plant (Al-Kahtani *et al.*, 2020). All these categories of bacteria possess different functions associated with plant growth promotion.

Endophytic bacteria are a specific group of rhizobacteria referred to as a subclass of rhizospheric bacteria that have the capability of invading the host plant tissues. Perotti (1926) reported that bacteria can infect and develop mutualistic associations with host plants during their special growth stage. These endophytic bacteria are isolated from surface-sterilized plant parts and do not harm the host plant economically. Endophytic bacteria affect the host plant growth positively and can exist above the ground, below the ground, and even in the seeds (Siddique *et al.*, 2022). In the case of habitat, endophytic bacteria occupy the plant endosphere as a protective ecological niche, which in turn facilitates these bacteria under unfluctuating environmental conditions. Endophytic bacteria also have a two-stage life cycle that goes back and forth between the soil and the plant. Different species of endophytic bacteria have been isolated from above- and below-ground plant parts, including leaves, stems, roots, tubers, nodules, ovules, and fruits (Yarte *et al.*, 2022). The roots have many bacterial species as compared to the above-ground plant parts. These bacteria can promote the growth of different plants, such as rice, tomato, potato, canola, wheat, and many others (Wu *et al.*, 2022). Many studies have been conducted to assess the growth-promoting effects of endophytic bacteria isolated from non-host plants. Some scientific researchers reported that endophytic bacteria only promote the growth of plants that are closely related to their natural hosts, but other researchers reported evidence of plant growth promotion in diverse plants (Vocciante *et al.*, 2022). However, in agricultural biotechnology, endophytic bacteria are considered a significant tool due to their wide host range, and that's why they are widely used as biopesticides

and biofertilizers for the development of safe, effective, and sustainable agricultural products.

Plant-associated bacteria: Plant-bacteria interactions have been studied for many decades (Fig. 1), indicating that plants can specify their microbiome or core of microbiome to obtain colonization with beneficial bacteria living inside host plant tissues, such as endophytic bacteria (Rädisch *et al.*, 2022). Hardoim *et al.* (2015) proposed the functional definition of endophytic bacteria, according to which any bacterium that can be isolated from the interior of plant parts or the disinfected surface of plant tissues without causing any noticeable damage to plant tissue is termed endophytic bacteria. In the case of ecological definitions, it is not obvious whether the residence of endophytic bacteria in plant tissues is beneficial for them or not, rather than living as phyllosphere bacteria (living on the aerial plant parts) or as saprophytes (living freely in the rhizosphere, e.g., rhizospheric bacteria) (Upadhyaya and Patel 2022). The rhizosphere is explained as the soil zone surrounding plant roots, which has a complex environment where plant roots interact with the soil chemically and physically. Furthermore, the rhizosphere is also stated as the soil area whose characteristics are affected by the physical presence and activity of the roots (Richardson *et al.*, 2009). For instance, in the case of normal root-soil interactions, soil nutrients (phosphorus) are supplied to roots through the rhizosphere or by the mycorrhizosphere before the acquisition of nutrients in the case of plant roots associated with mycorrhizal fungi. The biological composition and physiological characteristics of the rhizosphere are improved by the plants through various mechanisms, such as acidification by the release of root exudates and by the action of proton extrusion (Liu *et al.*, 2017a). Root exudates also affect the availability of nutrients for the plant, along with the change in soil pH.

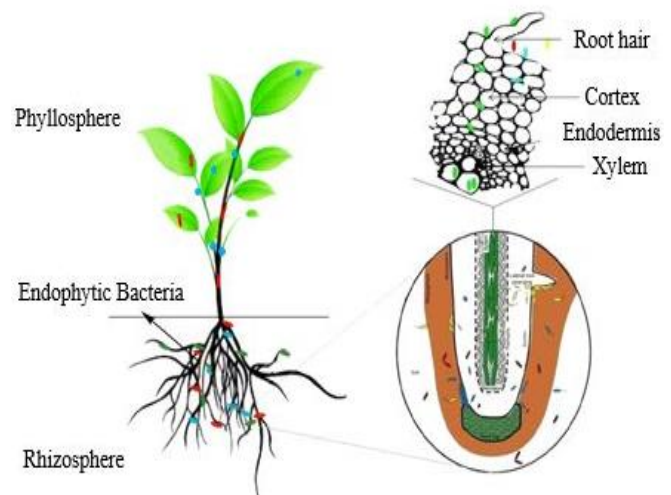


Figure 1. Presence and colonization of Bacterial endophytes within the host plant.



According to [Santoyo et al. \(2016\)](#), endophytic bacteria have more benefits than bacteria that colonize the rhizosphere and always remain in contact with plant cells by living within the plant tissues and therefore can immediately exert their beneficial impacts on host plants. However, in the case of plants, the root ecosystem is the main source for the colonization of endophytic bacteria because bacteria residing in the rhizosphere have the capability of entering and colonizing the plant roots ([Dandeniya et al., 2022](#)).

Rhizosphere colonization by endophytic bacteria:

Endophytic bacteria usually occupy space and get nutrients for colonization in the rhizosphere, which is a highly competitive task ([Santoyo et al., 2021](#)). [Santoyo et al. \(2016\)](#) reported that rhizosphere colonization and production of polysaccharides by endophytic *Azospirillum brasilense* and *Alcaligenes faecalis* are the most important bacterial characteristics. In rhizosphere soil, the bacterial rhizosphere population ranges from 10^7 to 10^9 cfu/g ([Mukherjee et al., 2021](#)), whereas the population of rhizosphere soil ranges between 10^5 and 10^7 cfu/g of fresh weight ([Chinakwe et al., 2019](#)). The system of bacterial detection based on immune markers, fluorescence in situ hybridization (FISH), and gfp or gusA-labeled strains has revealed that after inoculation, bacterial cells first colonize the rhizosphere ([Afzal et al., 2019](#)). Bacterial cells form a string of cells by adhering to the root surfaces. Moreover, bacterial species develop microcolonies and biofilms by colonizing the entire root surface and some rhizodermal cells ([Pu et al., 2018](#)). The colonization of rhizoplanes has been investigated in both types of plants growing in natural soils as well as in vitro. Endophytic bacteria, inhabiting the plant rhizosphere, must compete with other rhizospheric species for resources. To provide beneficial effects, bacteria must colonize the rhizosphere and the rhizoplane competently. In addition, the colonization of plant root systems by bacteria is not done in a uniform manner. For instance, [Gamalero et al. \(2009\)](#) reported that the density and distribution of *Pseudomonas fluorescens* strain A6RI varied during the colonization of the root zone of tomato plants. This non-uniform colonization is due to various factors that inhibit the process of root colonization, including motility and bacterial attachment, root exudation patterns, bacterial growth rate, bacterial quorum sensing, and minimizing the competition by acquiring nutrients efficiently and producing antagonistic substances ([Compant et al., 2010](#)). According to [Matilla et al. \(2007\)](#), these bacterial strains colonize the corn rhizosphere competently, where the bacterial genes associated with oxidative stress and metabolism are upregulated.

Root colonization by endophytic bacteria: Endophytic bacteria start to colonize the plant roots internally and develop bacterial sub-populations of about 10^5 to 10^7 cfu/g of fresh weight after their establishment in the rhizosphere and rhizoplane. The attachment of bacteria to the cell surface is mediated by pili, bacterial adhesion, and polysaccharides.

Once bacteria reach the root entry sites (on the root surface), such as wounds and lateral root emergence, by using the IV-type pili, they mediate the twitching motility ([Hori and Matsumoto 2010](#)). A diazotrophic endophyte, *Azoarcus sp.* BH72, colonizes the rice plant, resulting in the reduced colonization of rice roots as compared to wild-type bacteria because of a mutant defect in pilus retraction. All endophytic bacteria have distinct colonization preferences and patterns. Endophytic bacteria can enter the interior of host roots via specific or unique mechanisms. The process of host penetration may be of two types, namely active and passive ([Böhm et al., 2007](#)). In active penetration, competent endophytic bacteria use their machinery of attachment and proliferation/invasion, including the pili, flagella, quorum sensing, and twitching motility, to affect the colonization and movement of bacterial strains inside the host plant. Furthermore, cell wall degrading enzymes such as cellulases and pectinases are also secreted during the penetration and spread of endophytic bacteria in the host ([Rat et al., 2021](#)). Passive penetration, on the other hand, can occur at cracks in the root tips, root emergence areas, and those created or developed by the deleterious organism ([Synek et al., 2021](#)). For the identification of endophytic bacteria, two methods are used by the host plants: firstly, the formation of low cell densities (2–6 log cfu/gfw) as compared to the phytopathogenic bacteria (7–10 log cfu/gfw); and secondly, the production of lower levels of cell wall degrading enzymes than plant pathogens that are associated with high production quantities of these enzymes ([Zinniel et al., 2002](#)). So, the presence of endophytic bacteria in host plants is determined by genetic determinants of bacteria and chance factors, resulting in successful bacterial colonization through bacterial-plant crosstalk. For the selection of specific endophytic partners by the host plant, secretion of particular root exudates along with selective defense responses are considered the most significant selection factors ([Rosenblueth and Martinez-Romero 2006](#)).

Systemic colonization of aerial plant tissues by endophytic bacteria:

Once the endophyte gains entry inside the host it starts colonizing the host tissues. The endophytes in some cases remain close to their point of entry while in a few others get distributed systemically throughout the host plant. Under natural conditions, these bacteria develop leaf and stem populations ranging between 10^3 – 10^4 cfu/gfw ([Compant et al., 2010](#)). In the case of aerial colonization, only a few bacterial species are capable of invading the above-ground parts of the host plants because of various physiological factors required for the establishment of bacterial strains in these plant niches, but it is not clear that this aerial colonization in higher plants is as beneficial as root colonization ([Gómez-Lama et al., 2014](#)). Therefore, bacteria involved in aerial colonization are well adapted to these host plant niches. After entry, inside the host plant, bacterial movement is activated and supported by the plant transpiration stream and bacterial flagella. Different



cell wall degrading enzymes such as cellulase and anthered pectinases are secreted by the bacteria, which facilitates their movement along the intercellular spaces of the host cells. Furthermore, perforated plates are required for movement in xylem vessels, which allow the bacteria to move from large pores without the use of cell wall degrading enzymes. In the end, the final determination of bacterial strains is made in leaf tissues that are colonized by the plant roots. However, endophytic bacteria and plant pathogenic bacteria can also get into the leaf tissues through the phyllosphere with the help of leaf stomata.

Diverse bio-protective bacterial endophytes: From a variety of plant hosts, including agronomic crops, prairie grasslands, wild and perennial plants, as well as plants from severe habitats; endophytic bacteria have been identified and described (Afzal *et al.*, 2019). Both culturable and molecular studies have revealed a large species richness of plant-associated endophytic bacterial diversity. However, many studies conducted to check the diversity of bacterial endophytes are based on the study of those plant species that are cultivated in a broad area and have agronomical importance, including wheat (*Triticum spp.*), rice (*Oryza sativa*), maize (*Zea mays*), sugarcane (*Saccharum officinarum*), soy (*Glycine max*), potato (*Solanum tuberosum*) and some others. In their recent studies, Santoyo *et al.* (2016) enlisted some species of bacterial endophytes such as *Pseudomonas*, *Rhodanobacter*, *Micrococcus*, *Enterobacter*, *Stenotrophomonas*, *Rhanelia*, *Microbacterium*, *Pantoea*, *Bacillus*, *Arthrobacter*, *Sphingomonas*, *Methylobacterium*, *Phyllobacterium*, *Paenibacillus*, and *Burkholderia* that were widely present and associated with plant growth.

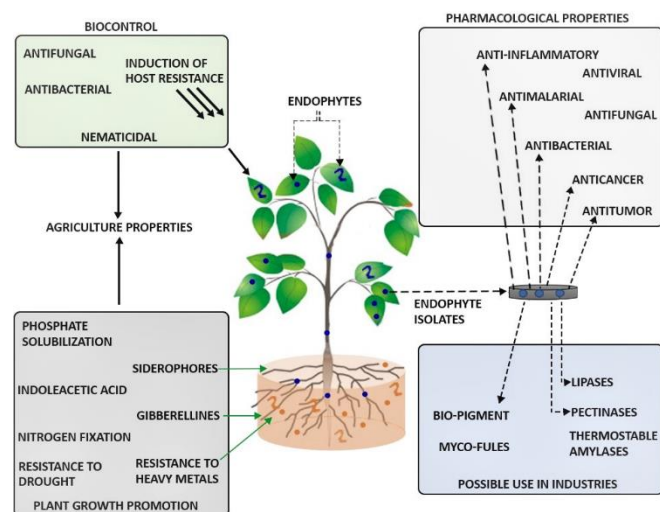


Figure 2. Beneficial aspects of Bacterial endophytes towards sustainable agricultural productions

Thus, it is suggested that ecologically rather than agronomically significant plants should be preferred for the

isolation of bacterial endophytes, especially in those areas where adverse environmental conditions are prevailing, and bacterial species need millions of years to establish a beneficial association with plants in such conditions. In a recent review report, Rincón and Neelam (2021) reviewed the endophytic bacterial diversity of common vegetables and fruits. They concluded that the most frequently isolated bacterial phyla from vegetables and fruits belonged to the genus *Actinobacteria*, *Bacteroidetes*, *Firmicutes*, *Proteobacteria*, *Pseudomonas*, *Sphingomonas*, *Methylobacterium*, *Bacillus*, *Arthrobacter*, *Pantoea*, and *Massilia*. Furthermore, different bacterial endophytic species have been isolated from important agricultural plants in numerous research studies (Table 1, Fig. 2) demonstrating the various bacterial-host benefits as well as antagonistic effects against many plant pathogens (Antunes *et al.*, 2022).

Biocontrol Mechanism: Bacterial endophytes, along with promoting plant growth, also exert inhibitory effects on the growth of plant pathogens (Table 1). This inhibitory effect is due to the production of many enzymes and antibiotic compounds that have antagonistic effects on plant pathogens and activate the plant defense system by the induction of systemic resistance (ISR) (Giannelli *et al.*, 2022). Also, they can easily take over the host plant and slow the growth of pathogens by competing with it for food and space. This makes plant diseases less common and less severe.

Antibiosis: Extensive studies have been conducted on the capability of bacterial endophytes to synthesize different antimicrobial compounds for the inhibition of the growth of plant pathogenic organisms along with their restriction and elimination. Santoyo *et al.* (2019) reported that *Bacillus* and *Pseudomonas* are the most studied genera of bacterial endophytes associated with the production of various antibiotics such as butyrolactone, aerugin, rhamnolipids, oomycin A, pyrroluteorine, zymicrolactone, kyanoamine, pyrrolinetrine, viscosinamide, ecomycins, cepacyamide A, phenazine-1-carboxamide, pseudomonic acid, cepafungins, phenazine-1-carboxylic acid, azomycin and 2,4-diacetylfloroglucinol acid. For the suppression of plant diseases, a wide variety of antibiotics are produced by the various strains of *Pseudomonas* (Paprocka *et al.*, 2021), including *P. fluorescence* associated with the production of 2,4-diacetylfloroglucinol and pyoluteorin, which are involved in the suppression of tobacco root rot caused by *Thielaviopsis basicola* (Morales-Cedeño *et al.*, 2021). Also, pyrrolnitrin, pioluteorin, and 2,4-diacetylfloroglucinol help reduce watercress disease caused by *Rhizoctonia solani* and *Pythium ultimum*, respectively, and 2,4-diacetylfloroglucinol helps stop the take-all disease of wheat (*Gaeumannomyces graminis*) (Milner *et al.*, 2019).

Lytic enzymes: The most important biological control of bacterial endophytes against plant pathogenic microorganisms, especially fungi, is the degradation of their cell walls by the production of enzymes (Jacob and Krishnan



2020). Fungal cell walls, along with those of plant pathogens, are made up of or composed of polysaccharides, glycoproteins, and some other components that vary according to the fungal species. 80% of the fungal cell wall is made up of polysaccharides, which provide stiffness to the cell wall through a network of glycosidic bonds (Zlotko *et al.*, 2019). When lytic enzymes interfere with the bonds of the fungal cell wall, they decompose the cell wall, leading to cell death (Abo-Elyousr *et al.*, 2021). The most abundantly secreted lytic enzymes that are associated with perforation, modification, and degradation of the structure of the cell wall are cellulases, proteases, 1,3-glucanases, and chitinases. Biological control of the black rot disease was reported by Mishra and Arora (2012) using *P. aeruginosa*, which produces chitinase (extracellular), and has an antagonistic effect on its bacterial pathogen (*Xanthomonas compestris*). Moreover, the biological management of *Pythium aphanidermatum* and *Rhizoctonia solani* is achieved by the actions of cellulases and chitinases produced by many strains of *Pseudomonas*, isolated from the chickpea rhizosphere. Similarly, biological control of *R. solani*, the causal organism of black scabies in the potato, is done using *Bacillus subtilis* through the release of chitinases (Saber *et al.*, 2015).

Induction of systemic response (ISR) in plants: Induced systemic resistance is a type of resistance that is introduced in plants against pathogens by the action of chemical signals (elicitors) produced by beneficial microorganisms (Yu *et al.*, 2022). ISR is introduced in plants by the chemical activation of a plant defense mechanism in which ethylene and jasmonic acid are involved. The molecular mechanisms that are involved in the chemical activation of the plant defense system by elicitors are pathogen-associated molecular patterns (PAMPs) or microbe-associated molecular patterns (MAMPs), various elicitors (siderophores, miRNAs, phytases, and volatile organic compounds), and phytohormones (Abdul *et al.*, 2020). In tobacco plants, the mechanism of ISR has been observed against *Phytophthora nicotianae* and *Rhizoctonia solani* by the action of PR2 (which encodes 1, 3 glucanases) and PR3 (which encodes chitinases), which were activated in response to volatile compounds produced by *Bacillus* (Kim *et al.*, 2015). Moreover, along with PR genes, some other protection mechanisms are also activated by the *Bacillus*, such as the production of secondary metabolites (such as auxins, glucosinolates, phytoalexins, and flavonoids) or structural changes or modifications in the cell wall by the deposition of lignin. Numerous endophytic bacterial strains such as *Bacillus* spp. *Bacillus amyloliquefaciens*, *Pseudomonas chlororaphis* and *Bacillus subtilis* are widely reported for management of charcoal rot disease (Chauhan *et al.*, 2022). Thus, activation of ISR has been shown to reduce the pathogenicity of many plant pathogens (viruses, bacteria, and fungi) in many crop varieties, including tomatoes, tobacco,

cucumbers, beans, radishes, and carnations (Kannoja *et al.*, 2019).

Production of δ -endotoxins: *Bacillus thuringiensis* (Bt) produced the endotoxins, which are made up of polypeptide units and have a molecular weight of about 27–140 kD (Villarreal-Delgado *et al.*, 2018). Cytolytic (Cyt) proteins are poisonous to many types of mammalian cells and to some insects in the order Diptera. In a similar way, most of the target or host organisms in the order Insecta react negatively to crystal (Cry) proteins. The mechanism of action of CRY proteins starts with their proteolysis by the action of proteases present in the midgut of the target host (Anaya *et al.*, 2020). Depending on the type of CRY protein, the separation of amino acids at the C-terminal and N-terminal regions leads to the release or production of active and toxic components that interact with receptor proteins in the intestinal cells of the host (insect), destroying the insect's intestinal epithelium by forming pre-pore oligomeric structures, which leads to the development of a lytic pore, which causes an osmotic imbalance and kills the insect. Recently, up to 13 strains of Bt-toxins have been used in agriculture, and some of them are facultative bacterial endophytes (Regnault-Roger *et al.*, 2012).

Siderophore production: Siderophores are receptor protein structures with high iron affinity and low molecular weight (400–1500 Da) produced by certain microbes in iron-limited environments. Siderophores act as iron sequestrants due to their high iron dissociation constant (between 1022 and 1055). Iron is used by biological control agents capable of producing siderophores via two mechanisms: (i) extracellular reduction of Fe into Fe²⁺ complexes, or (ii) directly through the cell membrane through the Fe³⁺ siderophores complex. Biological control agents regulate the iron concentration in host plants through sequestration (Fe³⁺ siderophore), resulting in the restricted growth of plant pathogens due to iron deficiency (Shah *et al.*, 2021). It has been reported that various bacterial strains are associated with the siderophores' production, resulting in the control of many plant diseases by limiting the growth and colonization of Fe-dependent plant pathogenic microorganisms (Lipková *et al.*, 2021; Wang *et al.*, 2022). Yu *et al.* (2011) found that the bacterial strain *B. subtilis* CAS15 produced catecholate-type siderophores (Bacillibactin), which acted against the growth of 15 fungal plant pathogens from the genera *Colletotrichum*, *Phytophthora*, *Fusarium*, *Magnaporthe*, and *Pythium*, slowing their growth by up to 94%.

Mechanism of Plant Growth Promotion: Endophytic bacteria form a symbiotic relationship with a host plant and provide benefits to it both directly and indirectly (Wang *et al.*, 2022). In direct mechanisms, endophytic bacteria promote plant growth by the production of growth-related hormones, which play an important role in the survival of plants in both normal and stressed conditions and by activating the availability of nutrients to the plants (Maheshwari *et al.*,



2022). However, indirectly, plant growth is promoted by the production of different chemical compounds and mechanisms antagonistic to the plant pathogens, such as the unavailability of nutrients to the pathogens, protecting the plants from future infections by activating the plant defense system, and the production of lytic enzymes and antibiotics (Enquahone *et al.*, 2022).

Nutrient acquisition: Soil is a growing medium used for the plantation of different crops, fruits, and vegetables, along with ornamental plants. The composition and structure of soil vary in different cultivation regions all over the world (Ali *et al.*, 2022b). The soils that are commonly deficient in one or more significant nutrients are considered the most important for plant growth. Different endophytic bacteria develop associations with plants and help in the availability of some nutrients such as phosphorus, nitrogen, and iron, which are deficient in these soils (Anuroopa *et al.*, 2022). The mechanisms for each nutrient are discussed here.

Nitrogen accessibility: Endophytic bacteria can increase the availability of nitrogen to plants in the form of fixed atmospheric nitrogen through the action of their nitrogenase activity. All nitrogen-fixing bacteria possess this nitrogenase enzyme, which is the highly conserved form of the protein (Enquahone *et al.*, 2022). Endophytic bacteria, according to Hurek and Reinhold-Hurek (2003), improve nitrogen availability to plants and promote plant growth and development in N₂-deficient soils much better than rhizospheric microorganisms. In addition, the rate of nitrogen fixation and its accumulation are also increased by the endophytic nitrogen-fixing bacteria in nitrogen-limited soils. However, for the activity of nitrogen fixation, root nodules associated with *Rhizobium* are more efficient than endophytic bacteria. However, an exceptional case is associated with the strains of *G. diazotrophicus* in their ability to fix nitrogen (Saranraj *et al.*, 2021). These strains have been isolated and identified as forming a symbiotic association with pine plants and sugarcane. Also, it has been found that the endophytic bacterium *Paenibacillus* strain P22 works well with a common tree and adds to the total nitrogen pool of the host plant (Wakarera *et al.*, 2022).

Phosphorus availability: Phosphorus is another major microelement and plays a significant role in the different enzymatic reactions involved in the various physiological processes of the plant. In soil, phosphorus may be present in ample or low quantities depending upon the soil quality, and mostly it is found in insoluble forms because of which it cannot be easily available to the host plants and can't support or improve their growth and development (Paz-Ares *et al.*, 2021). Endophytic bacteria, by using different mechanisms of solubilization such as chelation, the production of organic acids, ion exchange, and acidification, precipitate the phosphate and improve its availability to plants. The availability of phosphorus is also increased in the soil by the action of endophytic bacteria by releasing acid phosphatase,

which plays a crucial role in the mineralization of organic phosphorus (Mehrasa *et al.*, 2022). By assimilating the solubilized phosphorus, fixation and adsorption of phosphate under its limiting or restricted conditions are also prohibited by these bacteria. So, these bacteria are considered the reservoirs for the availability of this micronutrient to plants at the time of requirement. Phosphate solubilization is a major function of most endophytic bacteria (Rana *et al.*, 2021). There is a wide range of these bacteria associated with the 59–100% solubilization of mineral phosphate, isolated from sunflowers, soybean, strawberry, and cactus. The role of endophytic bacteria in phosphate solubilization was examined and reported by Puente *et al.* (2009) by carrying out a comparison of plants growing in sterile or controlled conditions with bacteria-free cacti growing on mineral phosphate supplemented with either nutrients or endophytes. In this experiment, plants failed to grow when cultivated on bacteria-free, unfertilized cacti, while the growth of inoculated plants was better without the addition of nutrients and comparable to fertilized plants. So, it was found that the plantlets that grew with endophytic bacteria only got a certain amount of nutrients.

Iron availability: Iron is another microelement required for most of the living organisms on earth. It is a part of various iron-containing proteins essential for the different physiological processes of the plant, such as respiration and transpiration (Ujvári *et al.*, 2021). It is present in the form of various ferric ions (Fe³⁺), including oxides, carbonates, phosphates of iron, and hydroxides, which occur in insoluble forms and are unavailable to plants. Endophytic bacteria produce iron-chelating compounds known as siderophores, which convert the unavailable form of iron to an available form (Verma *et al.*, 2021). These compounds (siderophores) are bound to ferric ions and increase their availability to plants by their movement through roots through the action of ligand exchange or chelate degradation. As a result, bacterial siderophores play an important role in the availability of iron to plants grown in iron-limited conditions and environments. An increase in the biomass of roots and shoots in maize was demonstrated by Marques *et al.* (2010), who described that the production of siderophores from endophytic bacteria is associated with these plants. Moreover, Radzki *et al.* (2013) reported the availability of iron in tomato plants grown in hydroponic culture due to the activity of bacterial siderophores. Along with the availability of iron to host plants, there are many other functions performed by endophytic bacteria by the production of siderophores, such as reducing the growth of plant pathogens by the depletion of iron by the activity of siderophores.

Phytohormone production and modulation: Endophytic bacteria are also involved in the production of certain plant growth-promoting phytohormones that play a vital role in metabolism and the availability of nutrients by host plants (Poveda *et al.*, 2021). Much of the recent research conducted



on the role of endophytic bacteria in the promotion of plant growth has shown that these bacteria are associated with an increase in plant biomass and nutrient uptake in plants colonized by such bacteria. The most significant phytohormones involved in plant-bacterial relationships are indole-3-acetic acid, ethylene, abscisic acid, gibberellins, and cytokinins (Xavier *et al.*, 2022).

Modulating plants indole acetic acid levels: The most important major plant hormone that is involved in various physiological processes in plants is indole acetic acid (IAA). It promotes plant development by inducing the plant defense system, signaling from one cell to another, biosynthesis of metabolites, activation of resistance to stress conditions, regulating stress responses, and initiating adventitious and lateral root development (Li *et al.*, 2022). It is also involved in the synthesis of other phytohormones, like ethylene. Endophytic bacteria play a critical role in the promotion of plant growth by the activation of the IAA pool because this is involved in the increased production of lateral roots and the promotion of surface area and root biomass (Huang *et al.*, 2022). The production of IAA from endophytic bacteria isolated from terrestrial orchids was also demonstrated by Tsavkelova *et al.* (2007). Initiation of root formation in kidney beans was reported by them due to the action of bacterial supernatant and the production of IAA, which was associated with the promotion of plant root systems by stimulating the number of developing roots and root length. Patten and Glick, (2002) also reported the vital role of bacterial IAA in the promotion of plant growth with the example of *Pseudomonas putida* GR12-2, which had no capability of increasing their root growth and lateral root formation due to the unavailability of IAA. Zúñiga *et al.* (2013), presented another example for demonstrating the condition of the plant root system without the function of IAA. They reported that mutant *Burkholderia phytofirmans* PsJN was not able to reduce the inhibitory effects in the roots of *Arabidopsis thaliana* caused by exogenous IAA as compared to wild-type strains due to the absence of IAA mineralization. Therefore, during the selection of beneficial bacterial endophytes, the production of IAA is considered an important factor. In addition, the decrease or increase in plant growth caused by the bacterial IAA is also estimated by the levels of plant IAA because the growth of plants with lower levels of endogenous IAA is distinctly increased by bacterial endophytes (Adeleke *et al.*, 2022).

Control of ethylene levels: Ethylene is a plant hormone that plays a vital role in the control of numerous physiological and developmental processes in host plants, such as abscission, fruit ripening, root nodulation, auxin transport, root initiation, cell elongation, and leaf senescence. It is also involved in the reduction of biotic and abiotic stresses. Levels of ethylene are increased because of different biotic and abiotic factors that result in the inhibition or reduction of the development of lateral roots, root hair formation, and elongation of roots

(Qian *et al.*, 2022). The enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase, which hydrolyzes the precursor of the plant hormone ethylene, is secreted by the endophytic bacteria. The endophytic bacteria involved in the breakdown of ACC can bind to the roots of plants, which results in the production of ketobutyrate and ammonia, which are used as nitrogen sources due to the cleavage of ACC. So, the hydrolysis or cleavage of ACC results in the promotion of plant growth under stress conditions due to the alleviation of plant stress. As reported by Rashid *et al.* (2012), many endophytic bacteria with the activity of ACC deaminase, are involved in plant growth promotion. In the case of canola, root growth of canola plants was not noticed to be promoted by the bacterium *B. phytofirmans* PsJN, which was inoculated in plants with its mutant gene of ACC deaminase, but the growth-enhancing/promoting ability of this mutant *B. phytofirmans* PsJN can be restored by the inoculation of a wild-type gene of ACC deaminase in the plants (Sun *et al.*, 2009). The beneficial impacts of all the above-mentioned bacteria on their host plants are related to the production of ACC deaminase.

Production of plant cytokinins and gibberellins: Endophytic bacteria are also associated with the production of gibberellins and cytokinins, which have different beneficial impacts on the host plants (Adeleke *et al.*, 2022). The impacts of *Azospirillum lipoferum* were reported by Cohen *et al.* (2009) on the maize plants that were treated with gibberellin inhibitors and were either provided with well-water or drought stress. Bacterial gibberellins are also involved in the removal of plant stress. In the same sense, likewise, two bacterial endophytes, including *Paenibacillus polymaxa* and *Pseudomonas resinovorans*, were studied by Bhore *et al.* (2010) and isolated from the *Gynura procumbens* by using the cucumber cotyledon greening bioassay used for the confirmation and identification of cytokinin-like compounds from the broth-extracts of these two endophytic bacteria.

Indirect growth promotion by suppression of phytopathogens: The growth of host plants is also indirectly induced or promoted by the endophytic bacteria by prohibiting the growth of plant pests and pathogens. Endophytic bacteria have antagonistic effects on both types of fungal and bacterial pathogens (Cui *et al.*, 2022). These endophytic bacteria, such as *Serratia*, *Bacillus*, *Actinobacteria*, *Pseudomonas*, *Enterobacter*, and *Paenibacillus*, are frequently influenced by antimicrobial properties (Palmieri *et al.*, 2022). Many bacterial substances that are involved in the indirect growth promotion of host plants, such as antimicrobial volatile organic compounds, toxins, antibiotics, siderophores, and hydrolytic enzymes, produced by endophytic bacteria, have significantly reduced the prevalence of fungal diseases in many crop plants, including wheat, black pepper, and potato. One of the mechanisms which are used by these beneficial endophytic bacteria for the prevention of their host plants from plant



pathogens is the induction of induced systemic resistance (ISR). The ISR induced by the endophytic bacteria is effective against all three types of bacterial, fungal, and viral pathogens (Harish *et al.*, 2022). The induction of induced systemic resistance protects non-interacted host proteins from future exposure to herbivorous insects and microbes by activating their defense mechanisms. In host plants, ISR by endophytic

bacteria is produced/introduced by a network of signaling pathways like ethylene-mediated pathways (ET) and chemical substances including jasmonic acid (JA) and salicylic acid (SA). Some genera of endophytic bacteria, such as *Serratia*, *Pseudomonas*, and *Bacillus*, are known to be associated with the activation of the plant defense system against pathogens by the induction of ISR (Singh *et al.*, 2022).

Table 1. Application of Bacterial Endophytes as PGP and BC agents.

Bacterial endophytes	Origin	Crop in use	Mechanism*	Reference
<i>Paenibacillus polymyxa</i> SK1	Bulbs of <i>Lilium lancifolium</i>	<i>Lilium lancifolium</i>	PGP, BC	Khan <i>et al.</i> (2020)
<i>Arthrobacter agilis</i> UMCV2	Strawberry	Strawberry	PGP	Hernández-Soberano <i>et al.</i> (2020)
<i>Stenotrophomonas maltophilia</i> strain UN1512	Strawberry leaves	Strawberry	PGP, BC	Alijani <i>et al.</i> (2020)
<i>Bacillus velezensis</i> 83	Mango	Mango	PGP, BC	Balderas-Ruíz <i>et al.</i> (2020)
<i>Staphylococcus seiuri</i>	<i>Psidium guajava</i> (Guava)	Guava	PGP (heavy metal resistance)	Riskuwa-Shehu <i>et al.</i> (2020)
<i>Herbaspirillum frisingense</i> strain IAC/BECa 152	Sugarcane roots	Sorghum	PGP	Kuramae <i>et al.</i> (2020)
<i>Bacillus</i> sp. Strain ESA 402	<i>Sorghum bicolor</i>	<i>Sorghum bicolor</i>	PGP	Santana <i>et al.</i> (2020)
<i>Enterobacter</i> sp. V1	cotton plant	Cotton	BC	Zhang <i>et al.</i> (2020)
<i>Bacillus amyloliquefaciens</i>	Apricot	Tomato	PGP, BC	Gautam <i>et al.</i> (2020)
<i>Pseudomonas palleroniana</i> Ps006	<i>Furcraea andina</i>	Banana (<i>Musa acuminata</i>)	PGP	Gamez <i>et al.</i> (2020)
<i>B. subtilis</i> strain xj-16	Roots of peach trees	Peach (<i>Prunus persica</i> L.)	BC	Chang <i>et al.</i> (2020)
<i>Burkholderia seminalis</i> Strain 869T2	<i>Chrysopogon zizanioides</i>	Lettuce and <i>Arabidopsis</i>	PGP	Hwang <i>et al.</i> (2021)
<i>Enterobacter hormaechei</i> sp.	Oil palm fruit	Okra (<i>Abelmoschus esculentus</i>) seedling	PGP	Roslan <i>et al.</i> (2020)
<i>Bacillus</i> sp. Strain EKM601B	Chinese okra	Okra	PGP, BC	Khalaf <i>et al.</i> (2020a)
<i>Bacillus</i> sp. Strains EKM417B	Watermelon	Watermelon	PGP, BC	Khalaf <i>et al.</i> (2020b)
<i>Bacillus velezensis</i> 8-4	Healthy potatoes	Potato	BC	Cui <i>et al.</i> (2020)
<i>Streptomyces leeuwenhoekii</i> KBT004	Tomato	Tomato seeds	BC	Athira and Anith (2020)
<i>Enterobacter roggenkampii</i> ED5	Sugarcane roots	Sugarcane	PGP, BC	Guo <i>et al.</i> (2020)
<i>Pseudomonas brassicacearum</i> CDVBN10	Rapeseed	Rapeseed	PGP	Jiménez-Gómez <i>et al.</i> (2020)
<i>B. cereus</i> SA1	Artemisia princeps	Soybean	PGP	Khan <i>et al.</i> (2020)
<i>Streptomyces</i> sp. Strain CBG9	Robusta coffee plant	Robusta coffee	BC	Hoang <i>et al.</i> (2020)
<i>Brevibacillus</i> sp.	Two native medicinal plants	<i>Zea mays</i>	PGP	Al-Kahtani <i>et al.</i> (2020)
<i>B. cereus</i> BI-8	<i>Pulicaria incisa</i>	<i>Zea mays</i>	PGP	Fouda <i>et al.</i> (2021)
<i>Bacillus thuringiensis</i> (BR1)	<i>Arthrocnemum macrostachyum</i>	Bean (<i>Vicia faba</i> L.)	PGP	Mahgoub <i>et al.</i> (2021)
<i>Pseudomonas</i> sp. M45	<i>Camellia sinensis</i>	Tea plant	PGP	Hazarika <i>et al.</i> (2021)
<i>Arthrobacter</i> sp.	<i>Cakile maritima</i> , <i>Matthiola tricuspidate</i>	<i>Cakile maritima</i>	PGP, BC	Christakis <i>et al.</i> (2021)
<i>Burkholderia gladioli</i> GI-6	Wheat	Wheat	PGP, BC	Shah <i>et al.</i> (2021)



Bacterial endophytes	Origin	Crop in use	Mechanism*	Reference
Strains of pseudomonas	Alkanna tinctoria roots	Hairy Roots of A. tinctoria	PGP, BC	Rat <i>et al.</i> (2021)
<i>Ewingella Americana</i> EU-M4ARAct	Maize	Maize seeds	PGP	Rana <i>et al.</i> (2021)
<i>Microbacterium laevaniformans</i>	Rice	Rice	PGP	Zhang <i>et al.</i> (2021)
<i>Sphingomonas</i> sp.	Roots and shoots of aromatic rice	Rice	PGP	Krishnamoorthy <i>et al.</i> (2021)
<i>Serratia plymuthica</i>	Chinese Leek	Apple	BC	Sun <i>et al.</i> (2021)
<i>Rahnella aquatilis</i> strain DST15	Apple (<i>Malus domestica</i> Borkh)	Apple	BC	Padder <i>et al.</i> (2021)
<i>Paraburkholderia tropica</i> IAC/BECa-13	Sugarcane plants	Sugarcane mini stalks	PGP	Cipriano <i>et al.</i> (2021)
<i>Nguyenibacter vanlangensis</i>	Sugarcane	Sugarcane	PGP, BC	Pitiwittayakul <i>et al.</i> (2021)
<i>Bacillus subtilis</i> subsp. <i>spizizenii</i> BL-59	Rice	Mango	BC	Duangkaew <i>et al.</i> (2021)
<i>Steroidobacter</i> sp.	Tobacco	Tobacco plants	PGP	Wang <i>et al.</i> (2021)
<i>Pantoea</i> sp.	Strawberry	Strawberry	BC	De Moura <i>et al.</i> (2021)
<i>Staphylococcus</i> sp.	Strawberry leaves	<i>Arbutus unedo</i> L.	BC	Martins <i>et al.</i> (2021)
<i>Sphingomonas zeicaulis</i>	-	Suaeda salsa	PGP	Guo <i>et al.</i> (2021)
<i>Erwinia persicina</i> EU-A3SK3	Foxtail millet	Chili	PGP	Devi <i>et al.</i> (2022)
<i>Proteobacteria</i> sp.	Albino tea leaves	Rice and tea	PGP	Jia <i>et al.</i> (2022)
<i>Bacillus subtilis</i> B9	Sugarcane	Sugarcane	PGP	Di <i>et al.</i> (2022)
<i>Pseudomonas gessardi</i> EU-LWNA-25	Crops growing in hilly regions of Himachal Pradesh	(<i>Amaranthus hypochondrius</i> L.	PGP	Devi <i>et al.</i> (2022)
<i>Alcaligenes faecalis</i> strain IG 27	-	Pea (<i>Pisum sativum</i>)	PGP	Sapre <i>et al.</i> (2022)
<i>Oceanobacillus jordanicus</i> Strain GSFE11	Durum wheat	Wheat	PGP	Alhindi <i>et al.</i> (2022)
<i>Shewanella putrefaciens</i>	Medicinal plant	Pearl millet seeds	PGP	Manjunatha <i>et al.</i> (2022)
<i>Bacillus amyloliquefaciens</i> (Pj2)	P. juliflora plant	Peanut	PGP	Kandi <i>et al.</i> (2022)
<i>Pseudomonas azotoformans</i> (E101)	Licorice plant	Licorice seed	PGP	Goudarzi <i>et al.</i> (2022)
<i>Bacillus subtilis</i> XZ16-1	Wheat	Wheat	PGP, BC	Yi <i>et al.</i> (2022)
<i>Providencia vermicola</i>	Tomato roots	<i>Luffa acutangula</i>	PGP	Tanveer <i>et al.</i> (2022)
<i>Nocardiopsis dassonvillei</i> (XIEG12)	<i>Thymus roseus</i>	Cotton	PGP, BC	Mohamad <i>et al.</i> (2022)
<i>Klebsiella</i> sp. HSTU-Sny5	Cauliflower and tomato roots	Eggplant	PGP	Das <i>et al.</i> (2022)
<i>Streptomyces</i> sp. B86	Sugar beet	Sugar beet	BC	Safara <i>et al.</i> (2022)
<i>Microbacterium oxydans</i>	Olive	Olive	BC	Mourou <i>et al.</i> (2022)
<i>Paraburkholderia</i> sp.	Tomato plants	Tomato	PGP	Helal <i>et al.</i> (2022)
<i>Pseudomonas</i> sp. Strain TE7	Common tamarisk	Barley and tomato seeds	PGP, BC	Bakelli <i>et al.</i> (2022)
<i>P. aeruginosa</i> strain FG106	Tomato plants	Tomato and potato	PGP, BC	Ghadamgahi <i>et al.</i> (2022)
<i>Enterobacter hormaechei</i> strain EMS16	<i>Musa acuminata</i>	<i>M. acuminata</i>	PGP, BC	Singh <i>et al.</i> (2022)
<i>Staphylococcus caprae</i>	Leaves of tomato, potato, and pepper plants	Chickpea seeds	BC	Nadeem <i>et al.</i> (2022)



Bacterial endophytes	Origin	Crop in use	Mechanism*	Reference
<i>Stenotrophomonas rhizophila</i> strain FT2	Glycyrrhiza uralensis seeds	Cucumber	PGP, BC	Wang <i>et al.</i> (2022)
<i>Sinorhizobium meliloti</i> (KBecto9p6)	Rice	Cucumber	PGP	Zapata-Sifuentes <i>et al.</i> (2022)
<i>Bacillus amyloliquefaciens</i>	Walnut trees	Persian walnut	PGP	Lotfi <i>et al.</i> (2022)
<i>Flavobacterium</i> sp	<i>Sedum alfredii</i> Hance	<i>Brassica juncea</i> L.	PGP, Cd tolerance	Wang <i>et al.</i> (2022)
<i>Brevibacillus</i> sp. Strain A9	Local chilli plant roots	Chili	PGP, BC	Aris <i>et al.</i> (2022)
<i>Bacillus</i> , <i>Stenotrophomonas</i> and <i>Pseudomonas</i>	Pot marigold rhizosphere	<i>Arabidopsis thaliana</i> and Tomato	PGP, BC	Tsalgatidou <i>et al.</i> (2023)
<i>Bacillus velezensis</i>	Maize roots	Maize	PGP, BC	Li <i>et al.</i> (2023)

*PGP: Plant Growth Promotion; BC: Biocontrol

Host specificity of growth-promoting endophytic bacteria:

Endophytic bacteria, in the case of their growth-promoting ability, are activated or influenced by the genotype of host plants, so they are host-specific. For example, *Solanum nigrum* is a host-specific bacterium and cannot promote the growth of a non-host plant like *Nicotiana attenuate*. Similarly, Kim *et al.* (2012) reported the growth promotion of switch grass (dependent on the host plant genotype) by the action or activity of *B. phytofirmans* PsJN. Furthermore, some endophytic bacteria have a wide host range, such as the PsJN strain of *B. phytofirmans*, isolated or extracted from onion roots, which is associated with the growth promotion of numerous plants, including potato, grape, wheat, switchgrass, maize, tomato, and *Arabidopsis thaliana*. Furthermore, the ability of endophytic bacteria to promote growth on host plants can be influenced by bacterial genotype. For example, the growth promotion of the same variety of potatoes by the different strains of *B. phytofirmans* has a pronounced difference in their activities (Trognitz *et al.*, 2008). In the same way, Dong *et al.* (1994) demonstrated four strains of endophytic *Salmonella enterica* that differently colonize and invade the hypocotyl and roots of alfalfa. Thus, the active processes of endophytic bacteria colonization and promotion of host plant growth are influenced and controlled by the genetic factors of both partners (the host plant and the endophytic bacteria). However, some other species of endophytic bacteria are involved in the growth promotion of non-host plants. Moreover, the growth of *Elsholtzia splendens* (the host) and *Brassica napus* (the non-host) in heavy metal-contaminated soils has also been shown to be promoted by the activity of copper-resistant species of endophytic bacteria such as *Bacillus megaterium* JL35 and *Burkholderia* sp. GL12 (Sun *et al.*, 2016). Some bacterial endophytes isolated from crop plants were known to be associated with the suppression of the disease effects of *Ralstonia solanacearum* on tomatoes (a non-host). Furthermore, some endophytic bacteria isolated from tomato plants grown on different agricultural soils could enhance the growth of canola plants under gnotobiotic conditions. Afzal *et al.* (2015) also reported the isolation of

some specific endophytic bacteria from the rhizosphere of *Cannabis sativa* through the use of canola.

Bacterial genes expressed in the endosphere: In endosphere colonization, bacterial endophytes promote the host's growth by using their various types of traits, properties, and characteristics (Wolska *et al.*, 2007; Azeem *et al.*, 2020). Some techniques are used for the confirmation of those properties, including gene introduction, real-time PCR, RNA-seq-based whole transcriptome profiling, gene complementation and deletion, in-vivo expression technology (IVET), the *gusA* fusion reporter system, and gene overexpression (Afzal *et al.*, 2019). The model endophytic bacterium that is used for these research studies is the PsJN strain of *B. phytofirmans*, which is associated with the growth promotion of numerous crops such as switchgrass, tomato, potato, maize, *Arabidopsis thaliana*, wheat, and grape by the colonization of the endosphere and rhizosphere. This strain (PsJN) is also involved in the promotion of plant tolerance against biotic stresses such as growth inhibition, restriction, and prevention of fungal plant pathogens and abiotic factors like drought and chilling stress (Sheibani-Tezerji *et al.*, 2015). For beneficial impacts, mechanisms used by the strain PsJN are quorum sensing, IAA degradation, and ACC deaminase. Furthermore, many growth-promoting traits about energy production, cellular homeostasis, transcription regulation, cell redox homeostasis, and general metabolism of lipids, sugars, nucleotides, and amino acids are shown by the bacterium during its growth within the host plant, which is determined by the expression profiling of plant genes. This study also revealed that during the stressful conditions of host plants, such as drought, some enzymes related to oxidative stress are secreted by the endophytic bacteria. These endophytic bacteria (strain PsJN) are also involved in the uptake and storage of iron (Galambos *et al.*, 2020). All the above-mentioned studies show that host plants only prefer their colonization by those endophytic bacteria that provide some benefits to plants in different conditions of a certain niche or habitat. For example, hydrocarbon-degrading/decomposing endophytic bacteria are only preferred by those host plants that are grown in areas or soils contaminated with



hydrocarbons. Moreover, endophytic bacteria also exert competitive effects on the bacteria occupying the endosphere of other host plants through immediate active penetration and systemic colonization of the host plant.

Bacteria Endophytes as a Major Source of Antimicrobial Secondary Metabolites

Antibiotics: The introduction of multi-resistant bacterial strains, a serious menace to clinical relevance is executing the scientists to formulate novel antibiotics. Regarding this, highly eco-adaptive and diverse bacterial endophytes are major sources of metabolites and novel antibiotics (Tyagi *et al.*, 2022). Endophytes are preferable as compared with soil microbes or epiphytes due to their effective communication, colonization, defense, and various secondary metabolites production. Moreover, these plant symbionts' emitted antibiotics are nontoxic to human beings and enhance plant host defense against various phytopathogens (Singh *et al.*, 2017; Zin *et al.*, 2017). They also repel the insects and nematodes injurious to plants. Recently, some new antibiotics secreted by endophytes residing in various plant species have been identified (Narayanan *et al.*, 2022).

Lipopeptides: Secondary metabolites of bacterial endophytes have a class known as Lipopeptides which are composed of short linear or cyclic peptides linked to lipophilic molecules. The most potent drugs can be commercially executed due to the antibiotic properties of lipopeptides toward various pathogens (Villarreal *et al.*, 2018). Three main classes of endophytic bacteria including pseudomycins, kakadumycins, and ecomycins have been characterized to secrete lipopeptides. Paenibacillus and Bacillus species are specified to produce lipopeptides. Such as *B. subtilis* and *B. amyloliquefaciens* are best source of lipopeptides. *B. subtilis* also releases polyketide antibiotics, particularly fengycin, bacillomycin, lichensyn, mycosubtilin, iturin, plipastin, surfactin, and pumilacidin (Ongena *et al.*, 2008). Most industrial antibiotics are manufactured by polyketides composed of small peptides. A large collection of metabolites produced by the endophytic Streptomyces sp. strain BT01 residing in *Boesenbergia rotunda* (L.) roots is strongly effective against *B. Cereus* and *B. Subtilus* (Taechowisan *et al.*, 2014). According to Jasim *et al.* (2016) lipopeptides having fengycin produced by *B. mojavensis* inhabiting *Bacopa monnieri* plants are found most successful against *S. typhi*, *E. coli*, *K. pneumoniae*, and *S. aureus*. A well-known cyclic lipopeptide, Fengycin is most efficient against bacterial strains that are resistant to many antibiotics (Lin *et al.*, 2020). The distinctive mode of action of cyclic lipopeptides makes them more effective as compared to conventional antibiotics.

Amino Acid-Rich Peptides: *P. viridiflava* is a leaf endophyte of various types of grasses, produces ecomycins (Miller *et al.*, 1998). These novel lipopeptides are linked with some unusual amino acids such as hydroxy aspartic acid and homoserine. These also have bonding with common amino acids such as serine, alanine, glycine, and threonine which are effective

against human fungal pathogens. Most common *Pseudomonas syringae* can produce pseudomycins, a polymer of non-traditional amino acids actively inhibits plant and human pathogenic fungi (Harrison *et al.*, 1991). Diverse environments donate unique endophytes with strong bioactive potential. For example, the medicinal plant *Plectranthus tenuiflorus* growing in arid and high-altitude environments contains bacterial endophytes that exhibit strong inhibition effects toward various pathogens including *K. pneumoniae*, *E. coli*, *S. typhi*, *Proteus mirabilis*, *S. aureus*, *Candida albicans*, and *Streptococcus agalactiae* (El-Deeb *et al.*, 2013). Moreover, the antagonistic relation and antibiotic resistance of endophytic bacteria vary according to various tissues of the same plant. This was concluded by research on endophytes of *Echinacea angustifolia*, *Origanum vulgare*, and *Echinacea purpurea*. These endophytic microorganisms could develop new mechanisms of antibiotic resistance and antibiotics (Narayanan *et al.*, 2022).

Cyclic Cationic Lipopeptides: Non-ribosomal peptide synthetase produces are produced by endophytic *Paenibacillus polymyxa* and exhibit effective inhibition against members of the *Enterobacteriaceae* family, including *Enterobacter* sp., *Shigella* sp., *E. coli*, *Citrobacter* sp., *Klebsiella* sp., and *Salmonella* sp. (Komura *et al.*, 1980; Stein 2005). Alvin *et al.* (2014) narrated PKS and NRPS gene products as effective in pathogen control. Recent studies on the medicinal plant *Origanum vulgare* L. reported four endophytes that produce paenicidin, polymyxins, and paeninodin. These antibiotics exhibited inhibition activities against ten strains of a *Burkholderia cepacia* complex causing inflammation of the cystic fibrosis. Three biogenetic gene clusters (BGCs) including NRP genes, lanthipeptide genes, and lassopeptide genes were identified by genomic analysis of these strains (Semenzato *et al.*, 2022).

Commercially available endophyte-based products: There are many products available on the market that are obtained from the endophytes isolated from the host plants and that play a vital role in the commercial production of agricultural crops (Aleynova *et al.*, 2022). The most important companies that are playing a leading role in the development of endophytes-based products are Agricon (New Zealand), GrassLans Technology Ltd. (New Zealand), Biotelliga Ltd. (New Zealand, Auckland), Intrinsyx Bio (US), and Adaptive Symbiotic Technologies (US) (Pandey *et al.*, 2022). For example, Epichloe is an endophytes-based product that is used in grassland farming systems in different countries, including the USA, New Zealand, Australia, and some parts of South America. BioEnsure, another endophyte-based product associated with 2–5 times increased seed germination rate during the cold season and 85% increased yield during the drought season in maize and rice, was developed by Adaptive Symbiotic Technologies (Seattle, Washington, US) and has been approved by the US Food and Drug Administration (FDA) and Department of Agriculture. At



present, BioEnsure is also being used on other crops and in other countries because it is also associated with a 25–50% decrease in water consumption in treated plants (Rodriguez *et al.*, 2019). Rootonic is another endophyte-based product that has been found to be effective for about 150 plants, such as angiosperms, gymnosperms, bryophytes, and pteridophytes, and forms a combination or mixture of *Piriformospora indica* biomass (endophyte) and magnesium sulfate (Murphy *et al.*, 2019). For ryegrass cultivation, successfully used products in New Zealand are NEA, NEA2, and NEA4. Furthermore, in the USA, South America, New Zealand, and Australia, different novel endophytes such as AR1TM and AR37TM for ryegrass and MaxQ for tall fescue cultivation have been used because these are associated with the production of insecticidal bioactive involved in the control of beetles, weevils, and aphids.

Multi-omics approaches are the future of the field, but conceptual frameworks should develop in parallel:

Nowadays, various omics tools and techniques have been developed to illustrate the host-related functional roles of different kinds of endophytic populations, including culture-omics, metagenomics, metabolomics, meta-transcriptomics, and meta-proteomics (Ali *et al.*, 2022a). The characteristics, limitations, and strengths of all these tools are deeply elaborated by Levy *et al.* (2018). These tools provide the immediate and significant heterogeneous datasets and high dimensions required for the coordination of useful information by utilizing advanced statistical approaches and bioinformatics. A number of molecular markers are used to check the variation and diversity of pathogens and different important agricultural crops (Ali *et al.*, 2022b). Shotgun metagenomics, by identifying the metabolic processes, characters, and genes required for endophytic nature, reveals the functions of endophytic bacteria. For example, in the case of sugarcane growth promotion, to identify the functions and metabolic pathways of endophytic bacteria that are exposed to apoplast fluid, a combination of proteomic and transcriptomic approaches was used by Terra *et al.* (2020). In the case of axenic plants inoculated with endophytic bacteria, omic strategies have been used in conjunction with other approaches such as confocal microscopy to identify that tissues are colonized by a bacterium and that it is actually an endophyte. Agtuca *et al.* (2020) used various techniques such as confocal and fluorescence imaging, as well as in situ metabolomics, to determine which types of metabolites are abundant in host plants inoculated with endophytes. In the future, there will be a need to use all the advanced approaches together because these "omic" techniques are not only the future of agriculture but also provide new discoveries of microbiological nature in the field. Moreover, along with the use of bioeconomy, technical developments, and fluxes of data, there is also a need to develop hypotheses in the areas of evolution and ecology to obtain advancement in the research of endophytes. In the end, the development of a conceptual

framework is required to check the effects of plant phenotype on the plant microbial community and vice versa, along with its application in space and time. These above-mentioned frameworks will require many other interdisciplinary approaches along with "omics" tools such as plant genetics and epigenetics, plant pathology, and physiology. At the global level, all of these things will give us a better chance to fully understand how plants evolved and how they work, as well as how they affect the environment through feedback.

Bacterial endophytes as nanoparticle biosynthesizers: The use of nanotechnology for disease management in the medical and agricultural sectors offers a secure and ecologically acceptable alternative to synthetic chemical agents (Ibrahim *et al.*, 2020). Nanoparticles are used in a wide range of scientific and medical sectors. Extensive therapeutic value, potential bioactivity, and non-pathogenic nature of nanoparticles have made their production and fabrication employing both bacterial endophytes came into being as new frontier technologies (Burrage and Jeon, 2021). Because using biological agents is one of the most economically viable, clean, and secure ways to create metal NPs, biological approaches are being used more frequently in the manufacture of metal nanoparticles. Endophytic involvement in the synthesis of nanoparticles opens up new possibilities for creating novel nanomaterials with a variety of uses (Rahman *et al.*, 2019). To combat metal ion toxicity, some endophytic bacteria have evolved a special defense mechanism. This method is based on the precipitation of metal ions at nanometer-scale to produce nanoparticles. Bacteria have an extraordinary ability to convert metal ions into nanoparticles, making them an ideal candidate for nanoparticle manufacturing. Endophyte-mediated nanoparticles may have antioxidant, antibacterial, antifungal, seed germination, and cytotoxic properties. The research of Syed *et al.* (2016) makes it possible to quickly and ecologically friendly produce gold nanoparticles using endophytic *Pseudomonas fluorescens* CA 417 that is found in *Coffea arabica* L. It was demonstrated that the gold nanoparticles had bactericidal effects on clinically important bacteria. Endophytic bacteria isolated from the medicinal plant *Coriandrum sativum* generated unique silver nanoparticles (AgNPs), which showed great potential in protecting rice plants against leaf blight and bacterial brown stripe infection, as well as boosting plant development. Bacteriological experiments revealed that the AgNPs were very active against the rice pathogenic bacteria *Xanthomonas oryzae* pv. *oryzae* (Xoo) strain LND0005 and *Acidovorax oryzae* (Ao) strain RS-1 (Ibrahim *et al.*, 2019). *Bacillus endophyticus* strain H3 used in synthesis of silver nanoparticles and may have antifungal properties against *Magnaporthe oryzae* and *Fusarium graminearum*. Overall, the results indicate that biosynthesized AgNPs may be capable of protecting plants from fungal diseases. Nanoparticles biosynthesized using endophytic bacteria are a potential option, according to the research, because they



exhibit a wide range of biological activities, including antioxidant and antibacterial characteristics.

Conclusions and future perspectives: Because of their beneficial aspects, endophytic bacteria are also being used as biopesticides and biofertilizers in agricultural soils for the better growth of economically important crops. But for some reason, they do not always promote the plant's growth efficiently. In this regard, the most serious issue is a failure to recognize the complex dynamics that govern the relationship between plant and endophyte. At the molecular level, the plant-endophyte association is carried out by some subtleties, which can be identified by the recognition of bacterial genes that are expressed by the bacterial endophytes in the host endosphere. The style of life adopted by endophytes in the endosphere of their host plants is achieved by conducting a detailed study on the bacterial transcriptome expressed by endophytes in host plants. This is done by an extremely difficult technique, such as the extraction of highly significant RNA transcripts from the surviving or growing bacteria. However, the extraction of these high-quality RNA transcripts is complicated because bacterial endophytes exist in hosts by forming low cell densities for their own survival and the inhibition of plant defenses. In host plants, preference for the colonization of themselves by endophytic bacteria is facilitated by some activities of endophytes recognized by bacterial meta-transcriptome analysis, which is a profile of community-wide global gene expression. The second factor that prominently influences the positive relationship between plants and endophyte is the plant or host genotype. For this purpose, some techniques and processes, such as vegetative growth and micro-propagation, are used to produce the genetically same clones of hosts to reduce the influence of host genotype on plant-endophyte associations. Thus, for more consistent field trials, plant-endophyte interactions can be performed earlier under controlled conditions than their transformation and transportation to field areas. Through the colonization of wild plants with specific bacterial endophytes, they are capable of survival under extreme biotic and abiotic conditions. Recognition of these bacteria is complicated, and their properties are identified by using both culture-independent and culture-dependent techniques collectively. The "green revolution" was introduced for the management of environmental problems, with advancements in two main categories. Firstly, improvements in the chemical inputs of crop plants, such as chemical fertilizers, pesticides, and herbicides. Secondly, techniques like genetic manipulation and targeted breeding were used to improve crop plants. However, the first category of the green revolution appeared to be harmful to the environment due to the repeated use of chemicals in agricultural soils. Thus, to solve the previous problems of the environment, there is a need to introduce a bio-revolution, or "fresh green revolution," through the application of antagonistic endophytic bacteria. Endophytic bacteria play a vital role in the management of pre-and post-

harvest plant diseases. In many conditions, it is assumed that the use of chemicals could be effectively reduced when endophytic bacteria are used along with chemical and physical treatments to increase or enhance the effectiveness of protection in vegetables and fruits against phytopathogens. Finally, to achieve long-term sustainable agricultural production, all these goals can be achieved by using comprehensive mechanisms and collaboration between industry and academia.

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